THE MALPIGHIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

KENNETH R. ROBERTSON

MALPIGHIACEAE A. L. de Jussieu, Gen. Pl. 252. 1789, "Malpighiae," nom. cons.

(MALPIGHIA FAMILY)

Trees, shrubs [or frequently lianas], typically with unicellular medifixed trichomes. Leaves opposite [rarely alternate or whorled; two glands often present toward the base of the blades or on the petioles], simple and mainly entire. Inflorescences terminal [or axillary], usually a many-flowered, simple to compound raceme or cyme with jointed 2-bracteolate pedicels. Flowers perfect [rarely polygamous, sometimes dimorphic or cleistogamous with certain parts abortive], ± regular [to irregular]. Sepals 5, free or united below, generally quincuncially imbricate in aestivation, each with two glands on the abaxial surfaces [or glands solitary, absent, on some sepals only, or decurrent on the pedicels]. Petals 5, free, predominantly clawed, mainly cochlear imbricate. Androecium obdiplostemonous, the stamens 10 [5 or 15, rarely fewer by abortion, sometimes reduced to staminodia]; filaments often basally united. Gynoecium of 3 [2, 4, 5] united [to free] carpels; ovary superior, each locule with a single hemianatropous ovule pendulous from an axile placenta; styles as many as the carpels, free [or united]; stigmas terminal [or sublateral].

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Fruit a drupe [berry, nut, samara, schizocarp, or capsule]; seeds with little or no endosperm; embryo circinate [or prevailingly straight to curved.] TYPE GENUS: *Malpighia* L.

A family of 55–65 genera and 700–1300 species largely confined to the tropics and subtropics with the greatest diversification in tropical America. Only *Heteropteris* HBK. is represented in both hemispheres, with about 80 species in the Americas and *H. leona* (Cav.) Exell in West Africa. *Byrsonima lucida* (Miller) DC. is the only species of the family in our area, but *Malpighia glabra* L., *Janusia gracilis* Gray, *Aspicarpa hyssopifolia* Gray, *A. longipes* Gray, *A. humilis* (Bentham) A. Juss., and *Galphimia angustifolia* Bentham (*Thryallis angustifolia* (Bentham) Kuntze; [2] closely related to, or perhaps better included within, *G. brasiliensis* (L.) A. Juss.; cf. MacBryde) occur in the southwestern United States.

The Malpighiaceae are often divided into two subfamilies, Malpighioideae (Planitorae Niedz.) and Gaudichaudioideae A. Juss. (Pyramidotorae Niedz., Hiraeoideae Scholz in Melchior, nom. inval.), which are subdivided into six tribes based primarily on fruit morphology. Only tribe Malpighieae (fruits drupes or 1–3-locular nuts) is represented in our area. The Malpighioideae are neotropical shrubs or trees with flat floral receptacles and unwinged fruits, while the Gaudichaudioideae are pantropical, mostly lianas, usually with pyramidal receptacles and winged or crested fruits. MacBryde, however, has reported 3-angled pyramidal receptacles in *Verrucularia glaucophylla* A. Juss., of the Malpighioideae-Galphimieae, and has suggested that a reëvaluation of the traditional subfamilial division is needed.

The current system of classification is that of Niedenzu, which was based on the system proposed by A. Jussieu. As noted by C. V. Morton, "Although Niedenzu's taxonomic work is detailed and careful, he apparently made up his rules of nomenclature as he went along. . . . Perhaps more than any other taxonomist, Niedenzu found it necessary to subdivide groups, and so in the larger genera there are numerous subgenera, each with sections, subsections, and series and subseries. It is doubtful that this plethora of names is really necessary." Because of the methodology of Niedenzu, and that of various other authors, the nomenclature of much of the family is chaotic, although many problems have been clarified by the recent works of Morton, MacBryde, and Cuatrecasas.

Generally aligned with families included by Engler & Prantl in the Geraniales, the Malpighiaceae, Polygalaceae, Trigoniaceae, and Vochysiaceae were included by Scholz, Cronquist, and Thorne in their Rutales, Polygalales, and Geraniales, respectively. Others ally the Malpighiaceae with the Linaceae, Geraniaceae, Zygophyllaceae, Erythroxylaceae, and re-

[2] *Thryallis* Martius (1829; type species: *T. longifolia* Mart.) has been conserved over *Thryallis* Linnaeus (1762; type species: *T. brasiliensis* L.) for a small Brazilian genus. Thus, the name *Galphimia* Cav. (1799; type species: *G. glauca* Cav.) can be used without conservation for an American genus of about ten species, even though it is a taxonomic synonym of *Thryallis* L. (cf. Taxon **16**: 76, 77. 1967; **17**: 328. 1968).

lated families. Takhtajan places this latter group of five families in his Geraniales (derived from the Rutales, Saxifragales, and Dilleniales), while Hutchinson includes them in the Malpighiales (derived from the Tiliales, Bixales, and Dilleniales). Cronquist considers the origin of the Geraniales, Linales, and Polygalales to be from the Rosales via the Sapindales.

A distinctive feature of the family, although by no means confined to it, is the "Malpighian" type of trichome, which is unicellular, two-armed, and attached by a more or less medifixed stalk. Unbranched, stellate, glandular, and stinging trichomes also occur in the family. Complex, somewhat fleshy, paired glands visible to the naked eye frequently occur on the outside of the sepals and on the leaf margins, lower leaf surfaces, or petioles. The stomata are paracytic, and the wood is commonly diffuse-porous with a tendency for the simple-perforated vessels to be aggregated into radial chains or clusters. The parenchyma is prevailingly paratracheal, and the multiseriate rays are heterogeneous. Although the anatomy of many lianous species is normal, some have highly complicated stelar structures.

The known chromosome numbers (of about 30 species in 14 genera) suggest that considerable diversification through polyploidy and aneuploidy has occurred. Reported sporophytic chromosome numbers are 12, 18, 20, 22, 24, 34, 38, 40, 42, 54, 56, 58, 72, ca. 84. More than one chromosome number has been reported in *Byrsonima crassifolia*, *Galphimia angustifolia*, possibly *G. glauca*, *Hiptage Madablota*, *Malpighia glabra*, and *Stigmaphyllon ciliatum*.

Two basic pollen types are found in the Malpighiaceae. In the first the grains are 3(4, 5)-colporate, with the colpal furrows distinct, united at the poles (syncolporate) or bibranched (parasyncolporate), while grains of the second pollen type are 4- to ca. 24-porate, often with complex geometric shapes correlated with the number of apertures, and with vestigial furrows forming surface patterns. In her study of African and Madagascan genera (including four American genera for comparison), Lobreau found correlations between pollen morphology and certain androecial and gynoecial features and indications that Malpighiacean pollen is similar to that of the Hypericaceae and Caryocaraceae. Erdtman found palynological similarities with the Humiriaceae, Tremandraceae, Trigoniaceae, and Zygophyllaceae. A thorough study of New World genera is needed for confirmation of a correlation of pollen morphology and the established subfamilial classification.

Although actual pollination has been observed only in *Malpighia*, *Bunchosia* L. C. Rich. ex HBK., and *Hiptage* Gaertner, the flowers of most genera appear to be "bee flowers." There are striking similarities between the flowers of certain Malpighiaceae and those of some species of *Oncidium* (Orchidaceae), but little has been published about this remarkable convergence. The floral mechanism of *Hiptage Madablota* is said to resemble that of *Aesculus* (Hippocastanaceae). Dimorphic to highly modified cleistogamous flowers occur in certain genera.

The embryo sac is usually tetrasporic, 16-nucleate and of the Penaea type. *Galphimia glauca* and *G. gracilis* have bisporic, eight-nucleate, Allium-type embryo sacs. Species of *Heteropteris* HBK., *Stigmaphyllon* A. Juss., *Banisteria*, *Hiptage*, and *Aspicarpa* L. C. Rich. that have been investigated show nucellar polyembryony with fertilization evidently not occurring. (Fertilization has been reported only in *Malpighia glabra*, but it probably occurs in *Tristellateia australis*.) Further studies are needed to ascertain the extent and effects of apomixis in the family.

Fossil materials, mostly leaves and fruits, allegedly representing Malpighiaceae have been reported from the Middle Cretaceous to the Pliocene. Unlike members of numerous other families that are primarily tropical today, the Malpighiaceae evidently did not occur in the paleoflora of the present-day Arctic Zone, although the family is recorded from the Tertiary flora of Europe.

The economic uses of members of the Malpighiaceae are few, considering the family's size. Extracts and infusions from certain species are used as narcotics, folk medicines, insecticides, pigments, and tanning agents. Certain South American Indian tribes, primarily in the Amazon and Orinoco river basins, prepare hallucinogenic infusions variously known as *caapi*, *ayahuasca*, *yajé*, *natema*, and *pinde* from species of *Banisteriopsis* C. B. Robinson ex Small. The most commonly used species is *B. Caapi* (Spruce ex Griseb.) C. V. Morton, which contains the β-carboline alkaloid bases harmine, harmaline, and *d*-tetrahydroharmine. Harmine has also been isolated from *B. inebrians* C. V. Morton and from *Cabi paraensis* Ducke, a species used as a folk medicine but evidently not as a hallucinogen. Such harmala alkaloids do not occur in *B. Rusbyana* (Niedz.) C. V. Morton, a species used as an additive in hallucinogenic beverages, but relatively high concentrations of N, N-dimethyltryptamine and traces of other tryptamines do occur. A narcotic drink is also made from *Tetrapteris methystica* R. E. Schultes, on which chemical studies have not yet been made. It seems likely that other genera and species of Malpighiaceae will be found to be used as narcotics, medicines, and poisons by aboriginal peoples.

The fruits of *Byrsonima*, *Bunchosia*, and *Malpighia* species are edible, and the drupes of *Malpighia glabra* L.,[3] Barbados or West Indian Cherry, Acerola, Cereza, contain exceptionally high amounts of Vitamin C, from 15 to 100 times the concentration found in oranges. This species is grown to some extent in Florida, Hawaii, and the West Indies, and vitamin tablets and frozen or canned juice made from the fruits are commercially available. The fibrous stems of *Heteropteris umbellata* and *Banisteria longifolia* are used for roping and basketry binding respectively. Strong and attractive wood used in furniture and construction is obtained from the arborescent species of *Byrsonima*. Many species are quite ornamental

[3] *Malpighia glabra* L. and *M. punicifolia* L. have been considered to be either conspecific or distinct, with the cultivated plants placed in either species or thought to be hybrids between them.

and are in cultivation in the tropics and in conservatories, although not to the extent that they deserve. Species of *Bunchosia*, *Byrsonima*, *Galphimia*, *Heteropteris*, *Malpighia*, and *Stigmaphyllon* are cultivated to some extent in Florida and southern California.

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Subfamily MALPIGHIOIDEAE

Tribe Malpighieae

1. **Byrsonima** L. C. Richard ex Humboldt, Bonpland & Kunth, Nov. Gen. Sp. **5**: ed. fol. 113, ed. qu. 147. 1822.[4]

Low spreading shrubs to small [or large] trees [rarely lianas], often much branched; bark warty [or smooth]; glabrescent, with the simple or T-shaped, often rust-colored trichomes largely confined to the younger parts [or the leaves, peduncles, pedicels and twigs densely pubescent]. Leaves opposite, glandless, simple, entire, usually coriaceous, sessile or shortly petiolate; petioles mostly stout; blades obovate-spatulate [or ovate to circular], the upper surfaces commonly glossy when alive but becoming glaucous upon drying; stipules axillary [or interpetiolar] and mostly connate, small and persistent. Flowers pedicellate, the pedicels jointed and 2-bracteolate, in terminal, many-flowered, simple racemes (occasionally compound at the base). Sepals 5, persistent, in anthesis the distal portion incurving between the petal claws and forming a constriction around the ovary and base of styles, the tips recurving; abaxial glands 2 on each sepal, contiguous, somewhat fleshy [or absent]. Petals 5, glabrous, subequal [to distinctly unequal], white to pink or red [or yellow], turning a deeper color with age; claws long, recurved; blades strongly concave, reniform to subcircular with undulate and ± entire [to slightly toothed] apices. Stamens 10, nearly equal in length, all bearing anthers; filaments thick, flattened and connate below, pubescent inside; anthers basifixed, 2-locular and introrse at anthesis, glabrous [or pubescent], connectives thick [and often forming prominent apical appendages]. Gynoecium syncarpous, 3-carpellate; ovary 3-lobed, conical [ovoid or globose], glabrous; styles 3, free, terminal, glabrous, slender, ± straight, tipped by the subulate stigmatic surfaces; receptacle flat or slightly concave, densely pubescent. Fruit a green, yellow, orange, red or brown globose [ovoid or conical] drupe, crowned by the persistent styles; stone solitary; pericarp rather thick and fleshy; endocarp hard, woody, pitted [or smooth], angular, 3-seeded, rarely fewer seeded by abortion. Seeds subglobose; embryo circinate, the cotyledons subequal, terete. Lectotype species: *Malpighia spicata* Cav. = *Byrsonima spicata* (Cav.) DC.; see J. K. Small, N. Am. Fl. **25**: 166. 1910.[5] (Name from Greek, *byrsa*,

[4] The generic name is usually attributed to L. C. Richard ex A. L. de Jussieu (1811). However, De Jussieu merely suggests that it might be possible to follow Richard's idea of separating *Malpighia* L. into three genera, *Malpighia, Byrsonima,* and *Bunchosia*; he does not indicate that he adopts this division. Also see discussion in MacBryde.

[5] Humboldt, Bonpland & Kunth referred *M. spicata* Cav. and seven other species of *Malpighia* to *Byrsonima* but did not make the formal transfers. It remains for a

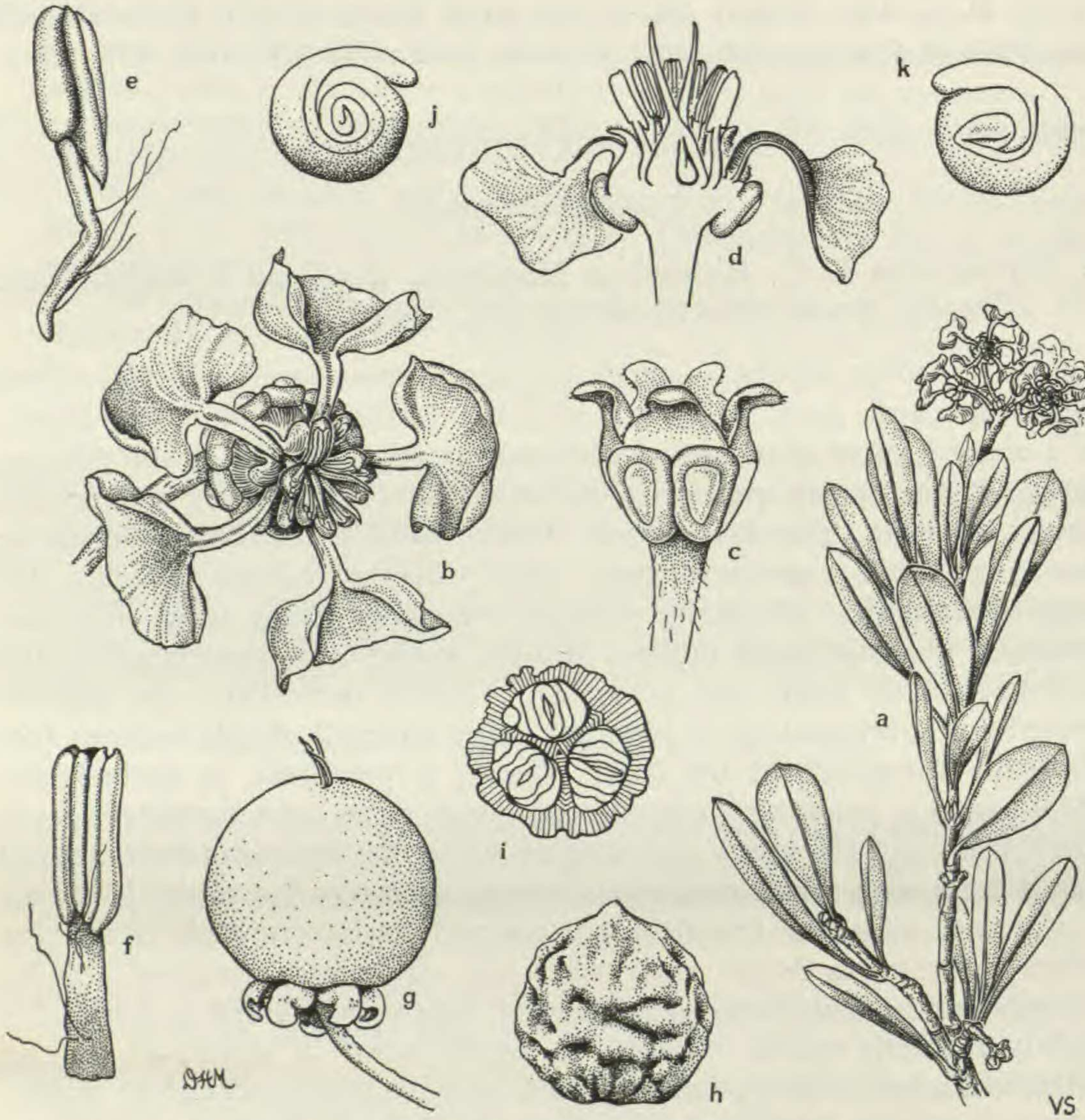

FIGURE 1. **Byrsonima.** a–k, *B. lucida*: a, flowering branch, × 1; b, flower, × 5; c, calyx, showing glands on one sepal (glands on adjacent sepals removed), × 7; d, vertical section of flower — ovule and placentation shown semidiagrammatically, × 5; e, oblique side-view of stamen with anther sacs (to right) protruding below enlarged connective (to left), × 14; f, adaxial surface of stamen showing four anther sacs, × 14; g, fruit, × 2; h, pitted stone of fruit, × 4; i, diagrammatic cross section of stone (hatched) showing an embryo in section in each locule, × 4; j, k, opposite sides of the same embryo to show position of cotyledons, oriented as in seed, × 6.

hide, and Latin *nimia*, very much (used), in reference to the use of the bark in tanning leather.)

A tropical American genus of more than 100 species ranging from southern Florida, the West Indies, and Mexico to Bolivia and southern

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monographer to determine whether this species chosen by Small can be considered to be part of the protologue and thus eligible to be the lectotype or whether one of the ten species described under *Byrsonima* would be a more appropriate choice.

Brazil. Many species grow in dry or harsh habitats such as savannas, rocky hills, coastal thickets, serpentine and palm barrens, and pinelands; other species occur in selvas (tropical rain forests) and montane or cloud forests. *Byrsonima*, *Alcoceratothrix* Niedz. (usually included in *Byrsonima*), *Diacidia* Griseb., *Burdachia* A. Juss., and *Glandonia* Griseb. constitute subtribe Byrsoniminae Niedz.

The genus is represented in our area by *Byrsonima lucida* (Miller) DC. (including *B. cuneata* (Turcz.) P. Wilson; cf. Sargent, 1921), locustberry, a plastic species varying in habit from low spreading shrubs less than a meter high to trees exceeding eight meters with trunks 25 cm. in diameter. Distinguished by small spatulate-obovate leaves, elongate inflorescences with small bracts, pinkish flowers, glabrous anthers, pubescent filaments, and connectives much shorter than the anther sacs, *B. lucida* occurs in pinelands, low woods, and hammocks in the Everglades and Florida Keys and throughout most of the West Indies from the Bahamas to Barbuda and Trinidad.

Following his penchant for subdividing taxa, Niedenzu (1928) divided *Byrsonima* into two subgenera, four sections, eight subsections, twelve series, and four subseries. In his system, *B. lucida*, along with three West Indian and six South American species, was placed in subgen. BRACHYZEUGMA, sect. SERICOLEPIS, subsect. *Psilotheca*, series *Dictyoneura*, subseries *Glossolepis*. The correct sectional name is EPIPHYLLARION Griseb.; C. V. Morton (1968) chose *B. lucida* as the lectotype of this section.

The genus needs a thoroughly documented modern taxonomic revision conducted on a broad geographic basis to delimit and classify the species and subgeneric taxa accurately and to apply the current rules of nomenclature uniformly.

Only *Byrsonima verbascifolia* (L.) DC. has been studied palynologically. The grains are 3-colporate with lalongate ora, prolate, rounded-triangular to subcircular in polar view, and with a reticulate exine. Similar pollen is found in tribe Galphimieae Niedz. Other genera of tribe Malpighieae which have thus far been examined (*Malpighia* and *Bunchosia*) have porate pollen.

Although quite ornamental, *Byrsonima lucida* is infrequently cultivated. *Byrsonima crassifolia* (L.) HBK., $2n = 20, 24$ (including *B. cotinifolia* HBK.; leaves large, elliptic or rarely somewhat obovate, flowers yellow to reddish), *B. coccolobifolia* HBK. (leaves large, subcircular to broadly ovate or obovate, flowers pink to red, connectives much longer than the anther sacs), and *B. spicata* (Cav.) DC. (leaves large, elliptic with acute apices, flowers yellow) are also grown to a limited extent in Florida.

The fruits of all *Byrsonima* species reputedly are edible, and some are sold in local markets in Latin America. The wood of arborescent species is strong and heavy, has a reddish color, and is used for furniture and construction or is converted into charcoal. Certain species are used in tanning leather, as a source of inks, dyes or paints, and in folk medicine as an astringent and for the treatment of wounds, fevers, colds, diarrhea, snake bites, and leg tumors!

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ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138